Table 2

Number of geographic regions in which shallow-water species of 21 families of gastropod mollusks have been recorded.

| Family | Number of regions | | | |
|---|---|---|---|---|
| | Three | Two | One | Total |
| Haliotidae | 4 | 1 | 1 | 6 |
| Trochidae | 14 | 7 | 4 | 25 |
| Turbinidae | 8 | 6 | 6 | 20 |
| Neritidae | 8 | 2 | 0 | 10 |
| Littorinidae | 12 | 3 | 13 | 28 |
| Strombidae | 30 | 7 | 3 | 39 |
| Naticidae | 15 | 6 | 4 | 25 |
| Cypraeidae | 58 | 14 | 15 | 87 |
| Cassidae | 9 | 1 | 1 | 11 |
| Tonnidae | 5 | 4 | 2 | 11 |
| Muricidae | 16 | 18 | 19 | 53 |
| Thaididae | 29 | 12 | 3 | 44 |
| Columbellidae | 9 | 3 | 3 | 15 |
| Nassariidae | 33 | 23 | 28 | 84 |
| Fasciolariidae | 14 | 8 | 5 | 27 |
| Olividae | 19 | 7 | 9 | 35 |
| Mitridae | 54 | 31 | 24 | 109 |
| Costellariidae | 34 | 32 | 29 | 95 |
| Volutidae | 2 | 9 | 21 | 32 |
| Conidae | 64 | 31 | 32 | 127 |
| Terebridae | 37 | 26 | 31 | 94 |
| Totals | 474 | 251 | 252 | 977 |

taxa now regarded as sibling species but alternatively possibly resulting in the separation of what is now considered to be one species into two or more. In view of these difficulties the figure of 16% for the gastropod families examined is not sufficiently large to justify the statement that the fauna of northern Australia is less diverse than the central area of the Indo-West Pacific.

The concept of a Tropical Australian Province is generally recognized (Endean, 1957; Marsh, 1976; Wells, 1986), but there are few data on the level of endemicity of marine groups in northern Australia. The level of endemicity required for a region to be considered distinct is arbitrary, but Briggs (1975) suggests a level of 10%. The data presented above show that 754 species of shallow-water gastropods in 21 families occur in northern Australia. At most 63, or 8%, are endemic to the north coast and one-third (21 species) belong to the single family Volutidae. Three-fourths (75%) of volute species examined are endemic to northern Australia. The next highest proportion of Australian endemics is in the littorinids with 27%. Volutes deposit their eggs in benthic egg masses from which the young hatch as crawling juveniles (Wilson & Gillett, 1971). The high proportion of volute species endemic to Australia is not surprising in view of the lack of a planktonic distributional phase in this group. Thus the shallow-water gastropods are near to, but below, the 10% level of endemicity required by Briggs (1975) to recognize the Tropical Australian Province.

Marsh & Marshall (1983) presented data on 376 shallow-water echinoderm species, 49 (13%) of which were regarded as endemic to northwestern Australia. The 1983 data contrast with the finding by Marsh (1976) only seven years earlier that 22 of 114 (19%) asteroid species examined were endemic to the state. Marsh & Marshall (1983) cautioned that with improved knowledge of the taxonomy of the species involved the level of endemicity might be further reduced. In such a short time the level of perceived endemicity has been reduced as knowledge of the fauna improved. This lower actual endemicity was confirmed by the report of Marsh (1986) of an additional 14 species of shallow-water echinoderms from northwestern Australia; all are Indo-West Pacific species. Wilson & Allen (1988) recently analyzed distributions of shallow-water fish in northern Australia. Of the approximately 2000 known species 13% are endemic to northern Australia. The data for the three major faunal groups show that the case for separation of the Tropical Australian Province from the remainder of the Indo-West Pacific is marginal. Hedley's (1926) concept of the north coast as a separate geographical province has been undermined in recent years by an increased understanding of the close relationship between the fauna of the north coast and the remainder of the Indo-West Pacific.

## ACKNOWLEDGMENTS

The ideas that form the basis of this paper were developed during a Fellowship at the Christensen Research Institute in Madang, Papua New Guinea, in 1987. I am grateful to CRI for the Fellowship and the staff, including particularly Dr. D. Christensen and T. Frohm, for help while there. Dr. G. Morgan of the Western Australian Museum is thanked for acting as a dive buddy on most dives. A considerable amount of information essential to the development of this paper was generated during collecting trips to atolls on the outer continental shelf of Western Australia during the 1980s. The trips were to Rowley Shoals in 1982 financed by the Western Australian Museum, Scott Reef and Seringapatam Reef in 1984 (Australian Marine Sciences and Technology Advisory Committee), and Ashmore Reef and Cartier Island in 1986 (Australian National Parks and Wildlife Service). All of the above expeditions were led by Dr. P. F. Berry; many of the mollusks were collected by C. W. Bryce and S. M. Slack-Smith. The inshore Kimberley was examined during a trip in 1988 funded largely by the National Geographic Society and Field Museum of Natural History, Chicago. C. W. Bryce also collected mollusks on this trip. The paper would not have been possible without the collections obtained during these expeditions. I am grateful to the funding agencies and colleagues on the trips for making them successful. I. Loch of the Australian Museum kindly provided access to their mollusk collections. Dr. P. A. Hutch-

ings of the Australian Museum critically read the manuscript and made a number of helpful suggestions. The manuscript benefited considerably from detailed comments made by two anonymous referees.

## LITERATURE CITED


ABBOTT, R. T. 1960. The genus *Strombus* in the Indo-Pacific. Indo-Pac. Moll. 1:33–144.

ABBOTT, R. T. 1961. The genus *Lambis* in the Indo-Pacific. Indo-Pac. Moll. 1:147–174.

ABBOTT, R. T. 1967a. The genus *Terebellum* (Gastropoda: Strombidae) in the Indo-Pacific. Indo-Pac. Moll. 1:445–454.

ABBOTT, R. T. 1967b. *Strombus* (*Canarium*) *wilsoni* new species from the Indo-Pacific. Indo-Pac. Moll. 1:455–456.

ABBOTT, R. T. 1968. The helmet shells of the world (Cassidae). Part I. Indo-Pac. Moll. 2:7–202.

BRATCHER, T. & W. O. CERNOHORSKY. 1987. Living terebras of the world. American Malacologists: Melbourne, Florida. 240 pp.

BRIGGS, J. C. 1975. Marine zoogeography. McGraw-Hill: New York. 475 pp.

BURGESS, C. M. 1985. Burgess' cowries of the world. Seacomber Publications: Capetown, South Africa. 289 pp.

CERNOHORSKY, W. O. 1976. The Mitridae of the world. Part I. The subfamily Mitrinae. Indo-Pac. Moll. 3:1–40.

CERNOHORSKY, W. O. 1984. Systematics of the family Nassariidae (Mollusca: Gastropoda). Bull. Auckl. Inst. Mus. 14: 1–356.

CLARK, H. L. 1946. The echinoderm fauna of Australia. Publ. Carnegie Inst. 566:1–567.

EKMAN, S. 1967. Zoogeography of the sea. Sidgwick & Jackson: London. 417 pp.

ENDEAN, R. 1957. The biogeography of Queensland's shallow water echinoderm fauna (excluding Crinoidea) with a rearrangement of the faunistic provinces of tropical Australia. Austral. Jour. Mar. Freshwater Res. 8:233–273.

HEDLEY, C. 1926. Zoogeography. Austral. Encyclop. 2:743–744.

HINTON, A. G. 1972. Shells of New Guinea and the central Indo-Pacific. Robert Brown: Port Moresby, Papua New Guinea. 94 pp.

HINTON, A. G. 1978. Guide to Australian shells. Robert Brown: Port Moresby, Papua New Guinea. 82 pp.

HINTON, A. G. 1980. Guide to shells of Papua New Guinea. Robert Brown: Port Moresby, Papua New Guinea. 73 pp.

KNOX, G. A. 1963. The biogeography and intertidal ecology of Australasian coasts. Oceanogr. Mar. Biol. Ann. Rev. 1: 341–404.

KNOX, G. A. 1980. Plate tectonics and the evolution of intertidal and shallow-water benthic biotic distribution patterns of the southwest Pacific. Paleogeography, Paleoclimatology, Paleoecology 31:267–297.

KREBS, C. J. 1978. Ecology. The experimental analysis of distribution and abundance. 2nd ed. Harper & Row: New York. 678 pp.

MARSH, L. M. 1976. Western Australian Asteroidea since H. L. Clark. Thalassia Jugoslav. 12:213–225.

MARSH, L. M. 1986. Part VI. Echinoderms. *In:* P. F. Berry, (ed.), Faunal surveys of the Rowley Shoals, Scott Reef and Seringapatam Reef, north-western Australia. Rec. West. Austral. Mus., Suppl. 25:63–74.

MARSH, L. M. & J. I. MARSHALL. 1983. Some aspects of the zoogeography of northwestern Australian echinoderms (other than holothurians). Bull. Mar. Sci. 33:671–687.

PECHAR, P., C. PRIOR & B. PARKINSON. 1980. Mitre shells from the Pacific and Indian Oceans. Robert Brown: Bathurst, New South Wales. 132 pp.

RADWIN, G. E. & A. D'ATTILIO. 1976. Murex shells of the world. Stanford University Press: Stanford, California. 284 pp.

REID, D. G. 1986. The littorinid molluscs of mangrove forests in the Indo-Pacific region. The genus *Littoraria*. British Museum (Natural History), London. 227 pp.

ROBERTS, D., S. SOEMODIHARDJO & W. KASTORO. 1982. Shallow water marine molluscs of north-west Java. Lembaga Oseanologie Nasional, Jakarta. 143 pp.

ROSEWATER, J. 1970. The family Littorinidae in the Indo-Pacific. Part I. The subfamily Littorininae. Indo-Pac. Moll. 2:417–506.

ROSEWATER, J. 1972. The family Littorinidae in the Indo-Pacific. Part II. The subfamilies Tectarinae and Echininae. Indo-Pac. Moll. 2:207–534.

SHORT, J. W. & D. G. POTTER. 1987. Shells of Queensland and the Great Barrier Reef. Golden Press: Drummoyne, New South Wales. 135 pp.

WALLS, J. G. 1980. Cone shells. TFH Publications: Neptune City, New Jersey. 1011 pp.

WEAVER, C. S. & J. E. DUPONT. 1970. The living volutes. Delaware Museum of Natural History, Greenville. 375 pp.

WELLS, F. E. 1980. The distribution of shallow-water marine prosobranch gastropod molluscs along the coastline of Western Australia. Veliger 22:232–247.

WELLS, F. E. 1986. Zoogeographic affinities of prosobranch gastropods of offshore coral reefs in northwestern Australia. Veliger 29:191–199.

WELLS, F. E. & C. W. BRYCE. 1986. Seashells of Western Australia. Western Australian Museum, Perth. 208 pp.

WELLS, F. E. & S. M. SLACK-SMITH. 1986. Part IV. Molluscs. *In:* P. F. Berry (ed.), Faunal surveys of the Rowley Shoals, Scott Reef and Seringapatam Reef, North-western Australia. Rec. West. Austral. Mus., Suppl. 25:41–57.

WHITLEY, G. 1932. Marine zoogeographical regions of Australia. Austral. Natur. 8:166.

WILSON, B. R. & G. R. ALLEN. 1988. Major components and distribution of marine fauna. Pp. 43–68. *In:* G. R. Dyne & D. W. Walton (eds.), Fauna of Australia. General articles. Australian Government Publishing Service: Canberra.

WILSON, B. R. & K. GILLETT. 1971. Australian shells. Reed: Sydney. 168 pp.

WILSON, B. R. & S. STEVENSON. 1977. Western Australian Cardiidae. West. Austral. Mus., Spec. Publ. 9:1–114.

ZIEGLER, R. F. & H. C. PORRECA. 1969. Olive shells of the world. Ziegler and Porreca: Henrietta, New York. 96 pp.

The Veliger 33(2):145-154 (April 2, 1990)

THE VELIGER


# New Records for Western Pacific *Morum* (Gastropoda: Harpidae) with Biogeographic Implications

by

WILLIAM K. EMERSON

Department of Invertebrates, American Museum of Natural History,
New York, New York 10024, USA

*Abstract.* Major extensions of the known range are reported for six species of the prosobranch genus *Morum,* namely: *M. teramachii, M. uchiyamai* and *M. joelgreenei* in the Mariana Islands, *M. uchiyamai* and *M. bruuni* in the region of New Caledonia, *M. cancellatum* in the Fiji Islands, and *M. kurzi* in the Solomon Islands. The distributional patterns of the 15 recognized species of *Morum* living in the Indo-West Pacific biogeographic region are evaluated in terms of the occurrences of these taxa on the regional lithospheric plates. The fossil and modern distributional patterns of *Morum* (*sensu lato*) suggest that these gastropods are remnants of a Tethyan faunal element which is limited in distribution owing largely to the apparent lack of teleplanic larvae.

## INTRODUCTION

This paper records major extensions of the known range for six Indo-Pacific species of the genus *Morum*. Specimens of *Morum teramachii* Kuroda & Habe, 1961, *M. uchiyamai* Kuroda & Habe, 1961, and *M. joelgreenei* Emerson, 1981, were obtained in the Mariana Islands by deep-water shrimp trapping operations of the NOAA vessel *Townsend Cromwell* during 1982 to 1984. This survey was conducted by the National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory as part of their Resource Assessment Investigation of the Mariana Archipelago Program (Emerson & Moffitt, 1988). Specimens of *Morum bruuni* (Powell, 1958) and *M. uchiyamai* Kuroda & Habe were dredged in 1986 off New Caledonia in deep water by the N.O. *Vauban* and N.O. *Coriolis,* vessels operated by the ORSTOM Center in Nouméa, New Caledonia (Bouchet, 1986; Richer de Forges, 1988). A single specimen of *M. kurzi* Petuch, 1979, was collected in 1985 by SCUBA diving from off Guadacanal in the Solomon Islands. A specimen of *M. cancellatum* B. G. Sowerby I, 1824, inhabited by a hermit crab was taken in a baited trap off Suva Reef, Fiji Islands, in 1979.

These new records significantly extend the known ranges of these taxa eastward along the Eurasian, Philippine, and Indian-Australian Lithospheric Plates to the western margin of the Pacific Plate.

## ABBREVIATIONS

The following abbreviations for institutions and organizations are used in the text.

AMNH—American Museum of Natural History, New York
BM(NH)—British Museum (Natural History), London
MNHN-Paris—Muséum National d'Histoire Naturelle, Paris
NMFSHL—National Marine Fisheries Service Southwest Fisheries Center, Honolulu Laboratory
NMNH—National Museum of Natural History, U.S. National Museum collection (USNM), Smithsonian Institution, Washington, D.C.
ORSTOM—Institut Français de Reserches pour le Développement en Coopération, Paris and Nouméa
TC—National Oceanic and Atmospheric Administration vessel *Townsend Cromwell*
UGMLM—University of Guam, Marine Laboratory, Mangilao, Guam
USBF—United States Bureau of Fisheries

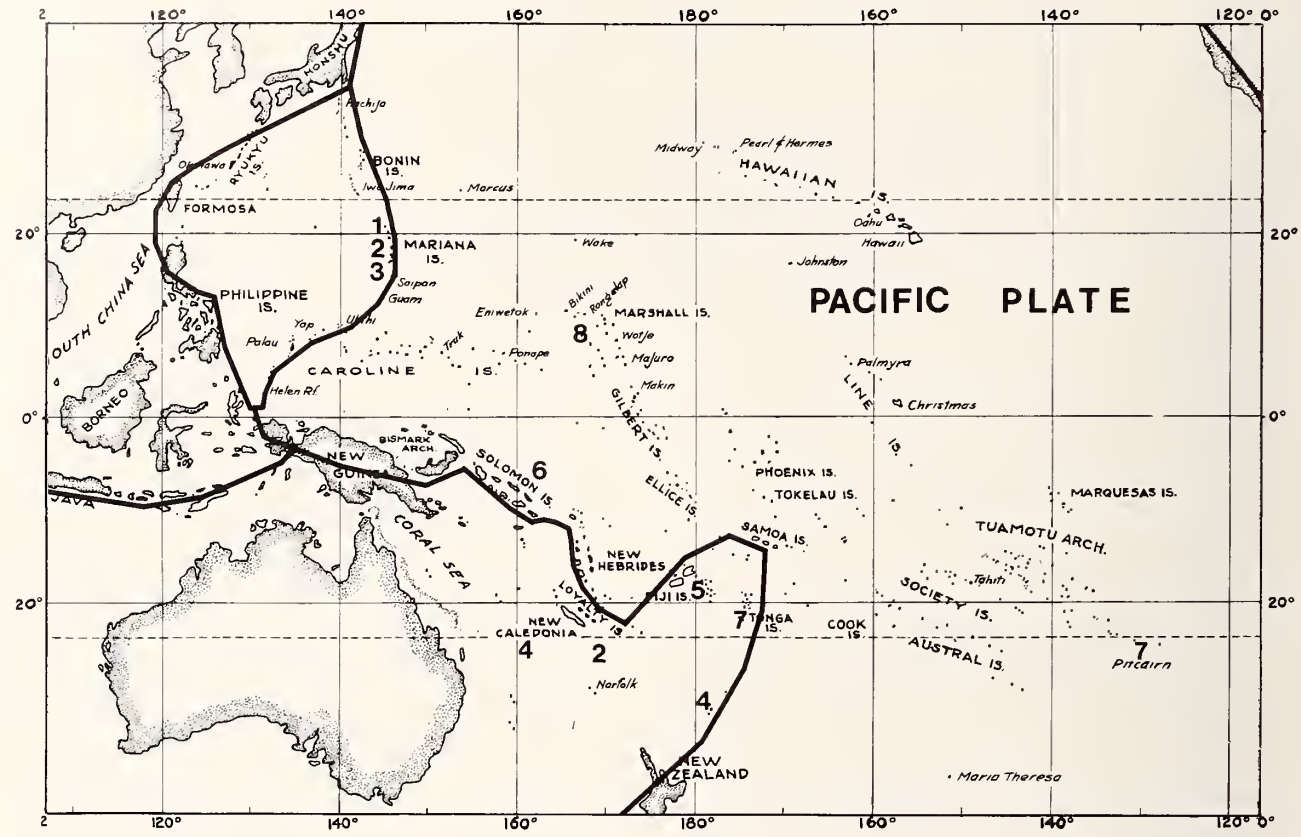



Figure 1

Distribution of *Morum* on the Pacific Plate (species numbers 6–8) and on or near the border of the Pacific Plate (species numbers 1–5, 7). 1 = *M. teramachii*, 2 = *M. uchiyamai*, 3 = *M. joelgreenei*, 4 = *M. bruuni*, 5 = *M. cancellatum*, 6 = *M. kurzi*, 7 = *M. ponderosum*, and 8 = *M. macdonaldi*. (Base map, without the plate boundaries, courtesy of R. T. Abbott.)

## SYSTEMATIC TREATMENT

Family HARPIDAE Bronn, 1849
Subfamily MORUMINAE Hughes & Emerson, 1987
Genus *Morum* Roeding, 1798
Subgenus *Oniscidia* Moerch, 1852

*Morum* (*O.*) *cancellatum* G. B. Sowerby I, 1824

(Figures 6, 7)

**New record:** FIJI ISLANDS: off Suva Reef (18.05°S, 178.25°E), Viti Levu in 220 m (120 fms), 21 March 1979, in baited *Nautilus* trap, 1 crabbed specimen, Roper and Sweeney collectors (USNM 773946).

**Remarks:** This record is based on a single, well-preserved, hermit-crabbed specimen, with fully developed apertural dentition and parietal shield (Figures 6, 7). The present specimen (44.1 mm × 27.5 mm) is slightly smaller than the lectotype, which measures 47.2 mm in height and 28.6 mm in width [BM(NH) 197744, EMERSON, 1985:54, figs. 17, 18], but is otherwise typical of this species.

**Range:** Previously known from southern Japan, Taiwan, the south China coast (off Pratas Island, in 161 m [88 fms], USBF Sta. 5111 (USNM 232801, USNM 237710), and the central Philippine Islands (Sandugan Pt., Signjos, Mindoro Island, AMNH 207315). Here recorded from the Fiji Islands in 220 m (dead specimen).

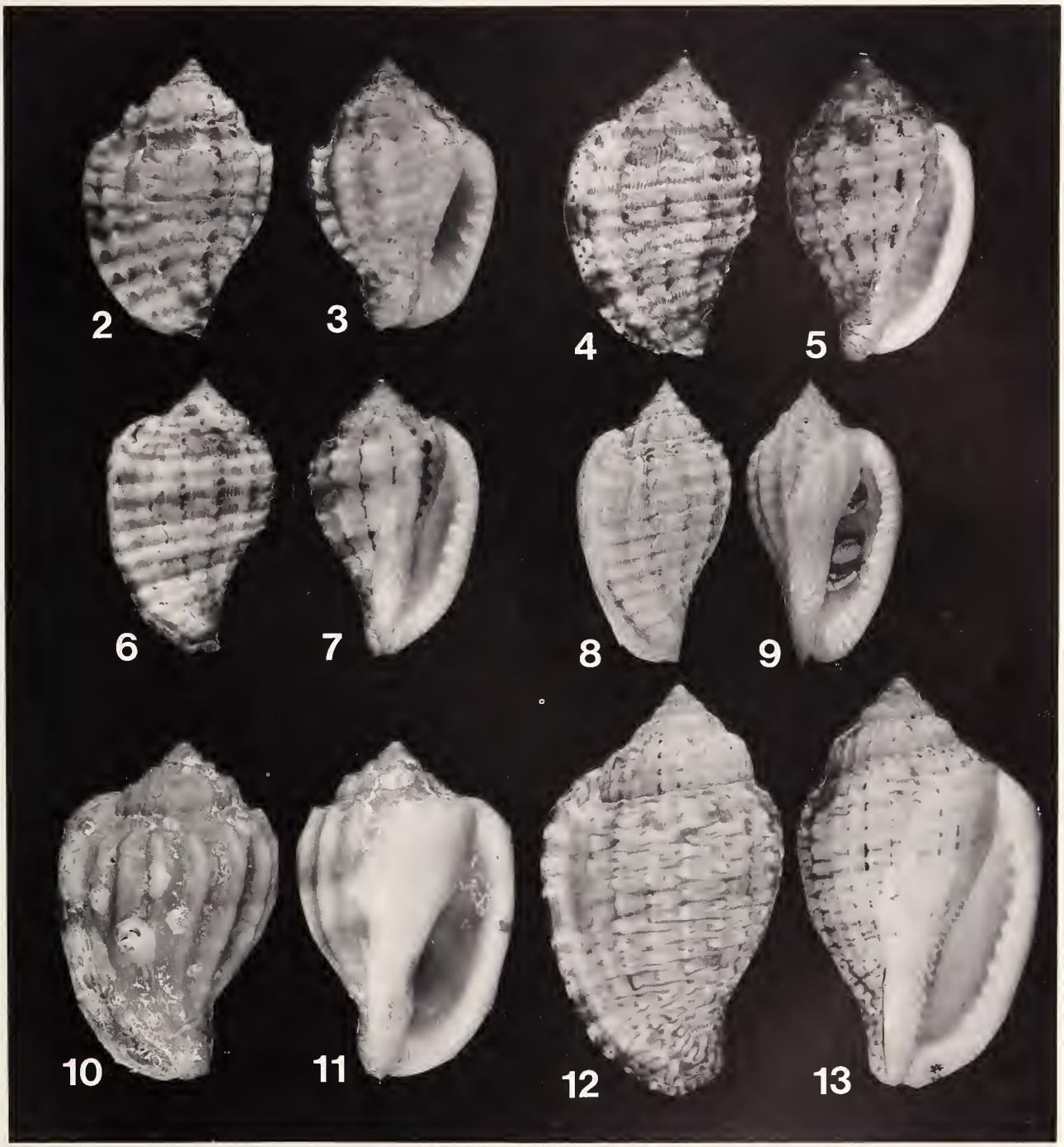
*Morum* (*O.*) *joelgreenei* Emerson, 1981

(Figures 4, 5)

**Synonym:** *M.* (*O.*) *celinamarumai* Kosuge, 1981 (see EMERSON, 1985: 52, pl. 1, figs. 9, 10). **Type locality:** "Bohol, Philippines."

**New record:** MARIANA ARCHIPELAGO: off Pagan Island (18°04.8′N, 145°45.2′E), in 201–284 m (110–150 fms), TC 84-02, Sta. 3, 20 February 1984 (AMNH 232122), from shrimp trap, 1 crabbed specimen.

**Remarks:** The present specimen (Figures 4, 5) is well preserved, but small (measuring 32 mm in length and 20.3




Explanation of Figures 2 to 13

Figures 2–13. Specimens representing the six taxa of *Morum* (*Oniscidia*) for which significant range extensions are recorded in this paper. Figures 2, 3: *M. kurzi* (AMNH 213436); ×2. Figures 4, 5: *M. joelgreenei* (AMNH 232122); ×1. Figures 6, 7: *M. cancellatum* (USNM 773946); ×1. Figures 8, 9: *M. uchiyamai* (AMNH 232123); ×1. Figures 10, 11: *M. bruuni* (Station DW71, MNHN-Paris); ×1.5. Figures 12, 13: *M. teramachii* (AMNH 232124); ×1.

mm in width) with an incompletely developed outer lip and an immature parietal shield.

**Range:** Previously known from moderately deep water (100 to 150 m) off the southern Philippine Islands. Here recorded from the Mariana Islands in deeper water (dead specimen).

*Morum* (*O.*) *kurzi* Petuch, 1979

(Figures 2, 3)

**New record:** SOLOMON ISLANDS: 1 km west of Honiara, Guadacanal Island, in 25–30 m (14–17 fms), spring of 1985, 1 specimen, by SCUBA diving, Johnson Kengalu collector (AMNH 213436).

**Remarks:** On a collecting trip to the Solomon Islands, Don Pisor obtained a single, live-collected specimen from a local diver (Figures 2, 3). It is typical of the Philippine specimens (type locality off Panglao, Bohol Island) and is essentially the same size as the holotype (EMERSON, 1985: 53, pl. 1, figs. 5, 6). The present specimen was generously donated to the AMNH by Mr. Pisor.

**Range:** Previously known only from the southern Philippines in depths of 110 (AMNH 213707) to 250 m (PETUCH, 1979). Here recorded from the Solomon Islands in lesser depths (25–30 m).

*Morum* (*O.*) *teramachii*
Kuroda & Habe *in* Habe, 1961

(Figures 12, 13)

**New records:** MARIANA ARCHIPELAGO: off Pagan Island (15°01′N, 145°14′E), in 366 m (220 fms), TC 82-04, Sta. 31, 3 August 1982 (AMNH 232126), from shrimp trap, 1 crabbed specimen; off Anatahan Island (16°21.6′N, 145°43.9′E), in 353 m (193 fms), TC 82-02, Sta. 47, 28 April 1982 (AMNH 232127), from shrimp trap, 2 live-taken specimens; off Farallon de Medinilla (16°08′N, 146°07′E), in 366 m (200 fms), TC 82-03, Sta. 104, 20 June 1982 (AMNH 232128), from shrimp trap, 1 crabbed specimen; off Arakane Reef (15°37.4′N, 142°46.2′E), in 311–476 m (170–260 fms), TC 83-05, Sta. 142, 15 December 1983 (UGMLM, No. 1; AMNH 232129, Nos. 3, 4), from shrimp traps, 4 crabbed specimens, No. 2 (AMNH 232124) here illustrated (Figures 12, 13); off Arakane Reef (15°37.6′N, 142°46.1′E) in 311–476 m (170–260 fms), TC 83-05, Sta. 151, 17 December 1983, USNM 869025, from shrimp trap, 1 crabbed specimen; off Esmeralda Island (15°01′N, 145°14′E), in 357–448 m (195–245 fms), TC 82-03, Sta. 39, 11 June 1982 (AMNH 232130), from shrimp trap, 1 crabbed specimen.

**Remarks:** The shells of the 10 specimens reported here range in measurements from 63.1 mm in length and 34.1 mm in width with 6½ post-nuclear whorls, to 40.9 mm in length and 26.4 mm in width with 5½ post-nuclear whorls. The figured type specimen of this taxon was stated to measure 55.5 × 32.3 mm and was dredged off Cape Ashiuri, Kochi Pref., Shikoku, Japan, in ca. 200 m (INABA & OYAMA, 1977:121).

**Range:** Previously known from southern Japan and the southern Philippine Islands (GLASS & FOSTER, 1986:68) in moderately deep water (100–200 m). Here recorded from the Mariana Islands, in depths of 170–448 m (live-taken specimens from 353 m).

*Morum* (*O.*) *uchiyamai* Kuroda & Habe
*in* Habe, 1961

(Figures 8, 9)

**New records:** MARIANA ARCHIPELAGO: off Saipan Island (15°15.83′N, 145°41.10′E), in 366–384 m (200–210 fms), TC 81-01, Sta. 179, 13 April 1981 (AMNH 232123), from shrimp trap, 1 crabbed specimen here illustrated (Figures 8, 9); off Esmeralda Bank (15°01.8′N, 145°13.7′E), in 384–430 m (210–235 fms), TC 84-01, Sta. 16, 8 January 1984 (UGMLM), from pipe dredge, 1 dead and discolored specimen. SOUTH OF NEW CALEDONIA: (22°53′S, 167°11′E) in 375–402 m (206–221 fms), N.O. *Vauban* SMIB2 cruise, Sta. DW15, 18 September 1986, MNHN-Paris, 1 crabbed specimen, Menou and Tirard collectors; (21°01′S, 167°27′E) dredged in 250 m (138 fms), R.V. *Alis* MUSORSTOM 6, Sta. DW453, 20 February 1989, MNHN-Paris, 1 live-collected specimen, Bouchet and Richer de Forges collectors.

**Remarks:** All three of the dead-taken specimens are smaller than the type specimen (51.5 mm × 27.5 mm), which was dredged off Kochi Pref., Shikoku, Japan, in 200–300 m (INABA & OYAMA, 1977:128). The live-taken New Caledonia specimen (52.2 × 28.4 mm) specimen is approximately the size of the holotype. The largest Marianan specimen (45.1 mm × 24.9 mm) is illustrated.

**Range:** Previously known from the region of the East China Sea (southern Japan and Taiwan) in moderately deep water (183–300 m). Here recorded in the Mariana Islands and in the region south of New Caledonia, in depths of 200–250 m (living specimens from 250 m).

*Morum* (*O.*) *bruuni* (Powell, 1958)

(Figures 10, 11)

**Synonym:** *Pulchroniscia delecta* Garrard, 1961 (see BEU, 1976: 225-229, figs. 1, 2, 4, 5, 11–15).

**New records:** CORAL SEA: off New Caledonia (22°48′S, 159°24′E), dredged in 360–390 m (198–215 fms), N.O. *Coriolis*, MUSORSTOM 5 Cruise, Sta. 299, 11 October 1986, MNHN-Paris, dead specimen encrusted with barnacles, etc., Bouchet, Metivier and Richer de Forges collectors. SOUTH OF NEW CALEDONIA: (24°42′S, 168°10′E), dredged in 230 m (127 fms), N.O. *Coriolis* CHALCAL 2

Cruise Sta. DW71, 27 October 1986, MNHN-Paris, 1 dead specimen, Bouchet, Metivier and Richer de Forges collectors (Figures 10, 11). (24°45'S, 168°09'E), dredged in 230 m (127 fms), N.O. *Coriolis* CHALCAL Cruise 2, Sta. CP20, 27 October 1986, MNHN-Paris, 1 dead specimen, Bouchet, Metivier and Richer de Forges collectors.

**Remarks:** The aperture of each of the three specimens shows some wear and the shells may have been occupied by hermit crabs after the death of the snails.

**Range:** Previously known only from moderately deep water (137–154 m) off southeastern Australia (New South Wales) and the Kermadec Islands (north of New Zealand). Here recorded from the Coral Sea and off New Caledonia, in depths of 230 and 390 m (based on dead specimens).

## BIOGEOGRAPHICAL CONSIDERATIONS

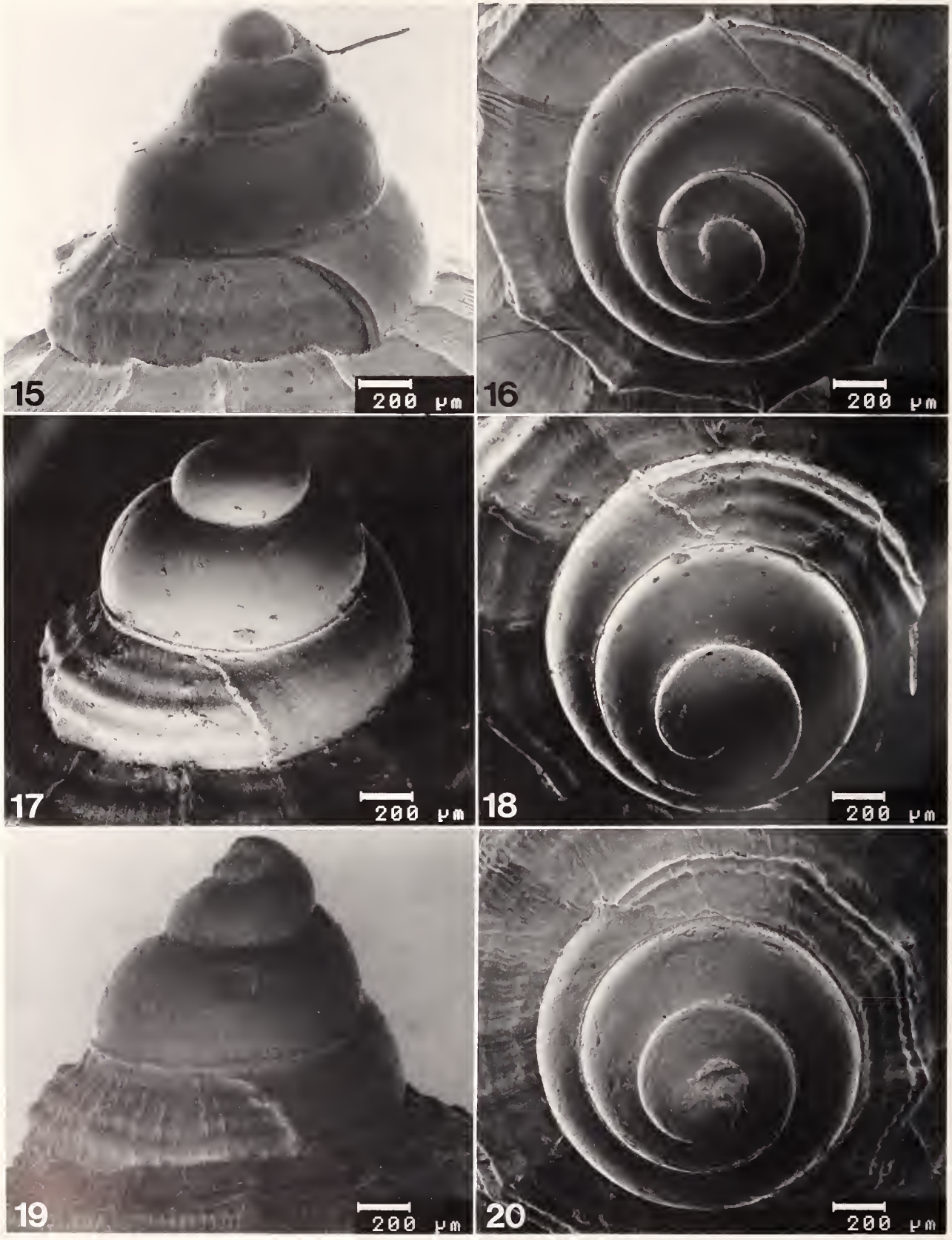
The genus *Morum* (*sensu lato*) was more widely distributed during the Tertiary with species known from the Paleogene of southern Europe, India, and Java, and from the Neogene of southern Europe, Japan, New Zealand, and the middle Americas. The surviving members of the subgenera *Oniscidia* and *Herculea* are most numerously represented in the western Pacific Ocean (see range data in Table 1). Here most of the species live at moderate shelf-depths to upper slope-depths, ranging from southern Japan, the Ryukyu Archipelago, Taiwan, and the southern Philippines. In the south Pacific, a few species are known from off southeastern Australia, New Zealand, New Guinea, New Caledonia, in the Solomon, Fiji and Tonga Islands, and at Pitcairn Island, occurring in depths of 25 to 350 m. Elsewhere in the Pacific Basin, a single species of *Oniscidia* is known in Micronesia (Marshall Islands) and two occur in the tropical eastern Pacific at Cocos Island and in the Galápagos Islands. One species of this subgenus is known from the western Indian Ocean and another in the Andaman Sea. The only other members of *Oniscidia* are known from the tropical western Atlantic, where three or four species are now recognized. *Morum* (*sensu stricto*) is limited to the New World tropics, with the oldest records dating from the Plio-Pleistocene. Three species of the nominate subgenus survive, two in the Caribbean region and one in the eastern Pacific, in shallow depths.

The fossil and modern distribution of *Morum* (*sensu lato*), therefore, suggests that these gastropods are remnants of a Tethyan faunal element with somewhat limited biological dispersal potential. Although data on larval development in *Morum* are meager, these gastropods apparently do not have teleplanic larvae. *Morum* (*Morum*) *oniscus* (Linnaeus, 1767) has a non-pelagic developmental mode. In this species, the large eggs are few in number and the juveniles emerge from the capsule at the crawling stage, with a protoconch of about 2.2 mm in height and with about 1½ to 2 nuclear whorls (Work, 1969:657, fig. 2; Hughes & Emerson, 1987:357, fig. 7). Living representatives of the subgenera *Oniscidia* and *Herculea,* however,

Figure 14

A living specimen of *Morum* (*O.*) *macdonaldi,* the only known "Pacific Plate" species of *Morum,* from Kwajalein Atoll, Marshall Islands; about 5 times natural size. (Drawing by Nancy Tunnell, 1988; courtesy of D. J. MacDonald.)

have larger multiwhorled protoconchs (Abbott, 1968:20, pl. 5). Some have 3 to 3½ nuclear whorls and a flared lip which demarcates the protoconch from the teleoconch (Figures 15–20). Dr. M. G. Harasewych examined the protoconch of a specimen of *M. kurzi* (AMNH 213707; Figures 15, 16) and inferred this species to be at least lecithotrophic with a limited pelagic phase and possibly planktotrophic, on the basis of the morphology of the protoconch. He concluded: "Analysis by Shuto's (1974) criteria [developmental mode inferred by ratio of the maximum diameter (D) to the number of protoconch whorls (VOL)] is inconclusive (VOL = 3.0; D = 1.41 mm; D/VOL = 0.47)" (Harasewych, *in litt.,* 15 May 1989). Dr. Rudolf S. Scheltema commented on the protoconchs of the three species figured herein as follows: "*Morum kurzi* (Figs. 15–16) has a planktotrophic veliger larvae as is inferred from the diameter of the apical protoconch whorl (ca. 220 $\mu$ by my measurement using the scale) and from the varix on the outer lip (which allows a rough estimate of size at settlement). The mode of development of *Morum bruuni* (Figs. 17–18) is less explicable; the rather large initial whorl (400 $\mu$) probably indicates a direct development, presumably within the egg capsule. *Morum ponderosum* (Figs. 19–20) also must have a planktotrophic veliger. Judging by the size at settlement (estimated from the SEM micrographs) both *M. kurzi* and *M. ponderosum* probably have a planktotrophic development of at least one month (probably even 2). While 2 months is somewhat less than that of most teleplanic larvae, it nevertheless will allow considerable opportunity for passive dispersal by advection of ocean currents and may explain why *M. ponderosum* occurs on Pitcairn Island (a geologically young island of


15
200 µm
16
200 µm
17
200 µm
18
200 µm
19
200 µm
20
200 µm

less than 1 my) for which otherwise there is no ready explanation" (Scheltema, *in litt.,* 19 July 1989). The restricted distributional patterns indicated for other species, however, may reflect the presence of temporally limited pelagic larval stages.

The occurrences on the lithospheric plates for the 16 nominal species of *Morum* living in the Indo-West Pacific biogeographical region are tabulated (see Table 1). One of these taxa, *M. watsoni* Dance & Emerson, 1967, a new name for *M. cithara* (Watson, 1881), not *M. cythara* (Brocchi, 1814), was based on an immature specimen for which the taxonomic status is not certain. Of the remaining 15 taxa, 10 occur on the Eurasian Plate, whereas 7 or possibly 8 of these extend onto the adjacent Philippine Plate, and 3 of these also occur on the Indian-Australian Plate. Two taxa are limited, respectively, to the Indian-Australian Plate and the African Plate, and two are restricted to the Eurasian Plate. The remaining taxa are of special biogeographical interest and are discussed in more detail below.

Only 3 of the 15 recognized species (20%) are known from the Pacific Plate (Figure 1). One of these, *Morum macdonaldi,* occurs only at Kwajalein Atoll, Marshall Islands, where living specimens have been observed by SCUBA divers in 15–30 m off the exposed side of fringing reefs (Figure 14). This is the only known "low island" species. It may have been overlooked elsewhere owing to the small size of the shells (10–18 mm) and to a nocturnal habit. The same circumstances may be true for *M. kurzi,* which is well known from the southern Philippines (Philippine Plate) in tangle-net collections and is reported here from 25–30 m at Guadalcanal Island, Solomon Islands (Pacific Plate). Populations of one species, *M. ponderosum,* are apparently isolated on the Pacific Plate at Pitcairn Island, where they occur in depths to 110 m (USNM 789326). This taxon is also known from the Tonga Islands (Cornfield, 1986:9), New Caledonia (Bouchet, 1981; BM[NH] 1964504), off Queensland, Australia (Beu, 1976:224) on the Indian-Australian Plate, and from the Ryukyu Archipelago (Emerson, 1977:85) on the Philippine Plate.

As indicated above, only 1 of the 15 western Pacific species (*Morum macdonaldi*) is restricted to the Pacific Plate (Figure 1) and, thus, can be termed a "Pacific Plate species" (*cf.* Springer, 1982; Kay, 1980, 1984; Newman, 1986; Briggs, 1987). In three cases—*M. teramachii, M. uchiyamai,* and *M. joelgreenei*—species occur on the eastern border of the Philippine Plate in the Mariana Islands, but the deep Mariana Trench apparently prevents the non-planktotrophic larvae of these gastropods from reaching the Pacific Plate. This is in contrast to the Mariana shoal-water faunal elements with apparent teleplanic larval development, which are believed to be a major source via a dispersal pattern for planktonically derived northwestern constituents in the Hawaiian fauna. As Vermeij *et al.* (1983) have noted, an offshoot of the Kuroshio Current forms a countercurrent and flows through the northern Mariana Islands, continues eastward to near Johnson Island, and eventually reaches the northwestern Hawaiian Islands (*cf.* Zinsmeister & Emerson, 1979). Thus, the Mariana Trench does not seem to be a barrier for passive dispersal of hemipelagic organisms that apparently have established Pacific Plate populations via the Marianas. The expansive deep-water barrier between the Mariana Islands and the Hawaiian Archipelago does, however, serve to select against the dispersal westward of certain molluscan groups, especially archaeogastropods and intertidal species (Vermeij *et al.,* 1983).

The Marianas apparently originated in the mid-Paleogene to the south and perhaps west of their present position, *i.e.,* closer to the Indonesian-Philippine arc systems (Karig, 1975). Accordingly, the distance required for dispersal of continental species to the proto-Marianas would have been reduced. Perhaps other islands (now subducted) on the Pacific Plate could have served as stepping stones for colonization by larval dispersal of the more westerly situated islands on the Pacific Plate during the Neogene (Springer, 1982).

The other two species of *Morum* known from the Pacific Plate are *M. kurzi* and *M. ponderosum* (Figure 1). The former occurs in the Solomon Islands adjoining the border of the Indian-Australian Plate. It is not known from the neighboring Bismarck Archipelago and the New Hebrides Islands (Vanuatu), which also border the Indian-Australian Plate. Collections from these areas, however, are not extensive. The vast Solomon Trench may act as a barrier for dispersal into the Melanesian region for species that undergo intracapsular metamorphosis or have a brief larval stage. The presence of *M. ponderosum* in the Tonga Islands on the far western border of the Indian-Australian Plate may reflect the survival of populations that were established on the Lau-Tonga Ridge, which may have been continuous with Kermadec Island Ridge (Springer, 1982). This ridge fronts a deep trench on the east face and extends southwestward to near New Zealand. This may have also served as the dispersal pathway to account for the presence of *M. bruuni* in the Kermadec Islands. *Morum cancellatum*

←

Explanations of Figures 15 to 20

Figures 15–20. Scanning electron micrographs showing lateral (left) and apical (right) views of three species of *Morum*; ×50. Figures 15, 16: *M.* (*O.*) *kurzi,* off Davao, Mindanao Island, Philippines (AMNH 213707). Figures 17, 18: *M.* (*O.*) *bruuni,* south of New Caledonia, 24°45′S, 168°09′E (MNHN-Paris). Figures 19, 20: *M.* (*H.*) *ponderosum,* off Seragaki Beach, Okinawa (AMNH 203693).

Table 1

Lithospheric Plate distribution of *Morum* in the Indo-West Pacific Tropics.

| | *n* = taxa per plate | | | | |
|---|---|---|---|---|---|
| | 1 African | 10 Eurasian | 9 Philippine | 6 Indian-Australian | 3 Pacific |
| Genus *Morum* Roeding, 1798 | | | | | |
| Subgenus *Oniscidia* Moerch, 1852 | | | | | |
| 1. *M. amabile* Shikama, 1973 | | | | | |
| Taiwan and ?Philippine Islands | | X | X | | |
| 2. *M. bruuni* Powell, 1958 | | | | | |
| SE Australia, off New Zealand and off New Caledonia | | | | X | |
| 3. *M. cancellatum* G. B. Sowerby I, 1824 | | | | | |
| Southern Japan to Philippine Islands, and Fiji Islands | | X | X | X | |
| 4. *M. exquisitum* (A. Adams & Reeve, 1848) | | | | | |
| Okinawa Island and southern Philippine Islands | | X | X | | |
| 5. *M. grande* (A. Adams, 1855) | | | | | |
| Southern Japan to Philippine Islands, Indonesia, and SE Australia | | X | X | X | |
| 6. *M. joelgreenei* Emerson, 1981 | | | | | |
| Southern Philippine Islands and Mariana Islands | | X | X | | |
| 7. *M. kurzi* Petuch, 1979 | | | | | |
| Southern Philippine Islands and Solomon Islands | | | X | | X |
| 8. *M. macandrewi* G. B. Sowerby III, 1889 | | | | | |
| Southern Japan | | X | | | |
| 9. *M. macdonaldi* Emerson, 1981 | | | | | |
| Marshall Islands | | | | | X |
| 10. *M. ninomiyai* Emerson, 1986 | | | | | |
| Off SW Thailand | | X | | | |
| 11. *M. praeclarum* Melvill, 1919 | | | | | |
| Off Somali Republic, SE Africa, Mozambique, and Seychelle Islands | X | | | | |
| 12. *M. teramachii* Kuroda & Habe *in* Habe, 1961 | | | | | |
| Southern Japan, Philippine Islands and Mariana Islands | | X | X | | |
| 13. *M. watanabei* Kosuge, 1981 | | | | | |
| Southern Philippines and possibly southern Japan | | X | ? | | |
| 14. *M. watsoni* Dance & Emerson, 1967 | | | | | |
| Kai Islands, off New Guinea | | | | X | |
| 15. *M. uchiyamai* Kuroda & Habe *in* Habe, 1961 | | | | | |
| Southern Japan, Taiwan, Mariana Islands, and New Caledonia | | X | X | X | |
| Subgenus *Herculea* Hanley *in* H. & A. Adams, 1858 | | | | | |
| 16. *M. ponderosum* (Hanley, 1858) | | | | | |
| Ryukyu Archipelago, Okinawa Island, SE Australia (Queensland), New Caledonia, Tonga Islands, and Pitcairn Island | | | X | X | X |

also occurs on the Indian-Australian Plate where it borders the Pacific Plate near the Fiji Islands. The apparent isolation of *M. ponderosum* on the southeastern Pacific Plate at Pitcairn Island could suggest a relict-faunal element, or more likely reflects larval recruitment from more westerly situated populations.

Bouchet & Poppe (1988:24–30) discussed the biogeographical significance of the volutid genera *Alcithoe* and *Lyria* in the New Caledonian region, where *Morum bruuni* and *M. uchiyamai* are here recorded. As appears to be the case for some of the species of *Morum*, these volutes apparently also have non-planktotrophic larval development. Bouchet & Poppe concluded that the Norfolk Ridge, which extends from New Zealand to New Caledonia, was a probable pathway for the dispersal of *Alcithoe*. In the case of *Lyria*, they presented a scenario for demersal dispersal, which seems unlikely at these depths (230–400 m), rather than one primarily based on vicariant events.

The genus *Morum* was recently allocated to the family Harpidae within a new subfamily, Moruminae (Hughes & Emerson, 1987; Emerson & Hughes, 1988). Both *Harpa* (Harpinae) and *Morum* have well-documented post-Tethyan fossil records, but *Harpa* may differ from *Morum* in the mode of development. The larvae of *Harpa*, in contrast to *Morum*, are believed to have an extended planktotrophic stage. In *Harpa*, the large capsules contain nu-